SURVIVAL OF *PAPILIO RUTULUS* LUCAS (LEPIDOPTERA: PAPILIONIDAE) LARVAE ON 42 POTENTIAL HOST PLANTS

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Abstract.—*Papilio rutulus* Lucas larvae completed development on 28 of 42 plant species in ten families. Tested plants included hosts previously reported for *P. rutulus* as well as a number listed for *Papilio eurymedon* Lucas, *P. glaucus* L. and *P. multicaudatus* Kirby. Egg to adult survival was highest on native western Salicaceae (*Populus* spp. and *Salix* spp.) (48.0–59.7%) with native western Rosaceae (*Prunus* spp. and *Amelanchier* spp.) next (25.0–31.7%). *Papilio rutulus* larval survival was more closely tied to the taxonomic relationship than to the relative abundance of these plants in central California. However, exotic host plants did not always follow the trends set by their native relatives. For example, exotic *Populus nigra* L. had the highest larval survival (75.4%) while exotic *Populus alba* L. had the lowest (4.0%) of the six *Populus* spp. tested.

Key Words.—Insecta, *Papilio rutulus*, *Papilio glaucus*, *Populus*, *Liriodendron*, host plant evolution, oviposition

Host plant affiliations of swallowtails in the *Papilio glaucus* L. species group (Monroe 1960) have been used to develop theories concerning the evolution of various species and subspecies in the group (Scriber et al. in press). The role of leaf chemistry in maintaining the differentation of various subspecies of *P. glaucus* plays a significant role in these theories (Lindroth et al. 1986, 1988). Previous research (Scriber 1988) has centered on the eastern members of the group as data on host plant utilization in the western members, *Papilio eurymedon* Lucas, *P. multicaudatus* Kirby and *P. rutulus* Lucas, is either scanty or contradictory (Brower 1958, Tietz 1971, Scott 1986). Determining which plants support complete development of these western swallowtails will be vital to our efforts to elucidate their evolutionary histories and the role of phytochemicals in maintaining any host plant separations that might exist.

The goals of this study were, therefore, to determine (1) whether *P. rutulus* larvae are able to complete their development on the various host plants cited in the literature for it and other members of the *glaucus* group, (2) whether exotic plants differ from their native relatives in their ability to support *P. rutulus* larvae and (3) whether the commonness of host plants in the environment influences their ability to support complete development of *P. rutulus* larvae.

MATERIALS AND METHODS

Papilio rutulus females were collected at various sites in Nevada, Sacramento, and Solano Counties, California, between Apr and Aug 1985–1990. Individual females were placed in 30.5 × 16.5 × 9 cm clear plastic boxes under an incandescent light with a minimum 14 h photophase. Each box had a moistened paper

Table 1. Scientific name, common name and family of the test plants.

Scientific name[a]	Common name	Family
Acer saccharinum L.	Silver Maple[b]	Aceraceae
Alnus oregona Nuttall	Oregon Alder[c]	Betulaceae
Alnus rhombifolia Nuttall	White Alder[c]	Betulaceae
Alnus tenufolia Nuttall	Mountain Alder[c]	Betulaceae
Betula occidentalis Hook	Water Birch[c]	Betulaceae
Betula papyrifera Marshall	Paper Birch	Betulaceae
Betula pendula Roth	European Birch	Betulaceae
Cornus serica L.	Creek Dogwood	Cornaceae
Quercus chrysolepis Liebmann	Canyon Oak[c]	Fagaceae
Cinnamomum camphora (L.)	Camphor	Lauraceae
Persea americana L.	Avocado[c]	Lauraceae
Liriodendron tulipifera (L.)	Tuliptree	Magnoliaceae
Magnolia accuminata (L.)	Cucumbertree[b]	Magnoliaceae
Fraxinus latifolia (Bentham)	Oregon Ash[b]	Oleaceae
Fraxinus dipetela Hooker & Arnott	Two-petel Ash	Oleaceae
Ligustrum japonicum Nuttall	Privet	Oleaceae
Syringa vulgaris L.	Lilac[c]	Oleaceae
Platanus californica Bentham	Sycamore[c]	Platanaceae
Rhamnus californica Eschscholtz	Coffeeberry	Rhamnaceae
Amelanchier alnifolia Nuttall	Serviceberry	Rosaceae
Fragaria chiloensis (L.)	Strawberry	Rosaceae
Malus sylvestris Miller	Apple[c]	Rosaceae
Prunus armeniaca L.	Apricot[c]	Rosaceae
Prunus ilicifolia (Nuttall)	Holly-lfd Cherry[c]	Rosaceae
Prunus lyoni (East)	Catalina Cherry	Rosaceae
Prunus subcordata Bentham	Klamath Plum	Rosaceae
Prunus virginiana L.	Chokecherry[c]	Rosaceae
Rubus leucodermis Douglas	Raspberry[b]	Rosaceae
Citrus limon (L.)	Lemon	Rutaceae
Ptelea crenulata Greene	Hoptree[c]	Rutaceae
Populus alba L.	Silver Poplar	Salicaceae
Populus angustifolia James	Nar.-lfd Cottonwood[c]	Salicaceae
Populus fremontii S. Watson	Fremont Cottonwood[c]	Salicaceae
Populus nigra L.	Lombardy Poplar	Salicaceae
Populus tremuloides Michanux	Trembling Aspen[c]	Salicaceae
Populus trichocarpa Grey	Black Cottonwood[c]	Salicaceae
Salix hindsiana Bentham	Sandbar Willow	Salicaceae
Salix lasiolepis Bentham	Arroyo Willow[c]	Salicaceae
Ribes aureum Pursh	Current	Saxifragaceae
Tilia americana L.	Basswood	Tiliaceae
Ulmus americana L.	American Elm[b]	Ulmaceae
Ulmus parvifolia Jacquin	Chinese Elm[b]	Ulmaceae

[a] Per Munz (1968) or Hortus Third if not in Munz.
[b] Listed as a host of *P. rutulus* by genus (see text).
[c] Listed as a host for *P. rutulus* by species (see text).

towel on the bottom and contained a bouquet of *Salix lasiolepis* Bentham leaves. The cut end of the bouquet was placed in an aquapic® to maintain leaf turgor. Twice daily each female was allowed to feed to satiation on a 1:4 honey:water solution. Eggs were removed every 1–2 days and placed in 10 × 100 mm petri dishes for incubation at 23.1 ± 1° C. Newly eclosed first instar larvae were placed on a turgid bouquet (Scriber 1977) of test plant leaves in a 25 × 140 mm petri

Table 2. Host plant specific survival of *P. rutulus* larvae.

Plant	Number larvae	Number adults	% survival	Abundance[a]
Populus nigra[b]	88	69	78.4	common
Populus angustifolia	54	32	59.3	rare
Populus tremuloides[c]	58	32	55.2	uncommon
Salix lasiolepis	49	27	55.1	very common
Populus trichocarpa	50	24	48.0	common
Populus fremontii[c]	50	24	48.0	common
Malus sylvestris[b]	37	12	32.4	common
Prunus lyoni	41	13	31.7	rare
Betula pendula[b]	39	12	30.8	very common
Prunus ilicifolia	55	16	29.1	rare
Prunus subcordata	4[d]	1	25.0	uncommon
Prunus virginiana	4[d]	1	25.0	common
Amelanchier alnifolia	26	6	23.1	rare
Fraxinus latifolia	41	6	14.6	uncommon
Betula papyrifera[bc]	7[d]	1	14.3	rare
Alnus oregona[c]	57	8	14.0	rare
Prunus armeniaca[b]	30	3	10.0	common
Citrus limon[bc]	60	5	8.3	very common
Alnus tenufolia	25	2	8.0	rare
Tilia americana[bc]	28	2	7.1	rare
Platanus californica[c]	53	3	5.7	common
Ligustrum japonicum[b]	40	2	5.0	very common
Liriodendron tulipifera[bc]	95	4	4.2	common
Populus alba[b]	50	2	4.0	uncommon
Cinnamomum camphora[b]	51	2	3.9	very common
Salix hindsiana	53	2	3.8	very common
Syringa vulgaris[b]	27	1	3.7	uncommon
Betula occidentalis	30	1	3.3	uncommon
Total	1177	315		

[a] As per Little (1976, 1984), Munz (1968), Anonymous (1988), and Griffin & Critchfield (1976).
[b] Plant exotic to California.
[c] Supported survival of first instar larvae (unpublished data).
[d] Insufficient plant material to test more larvae.

dish whose bottom was lined with filter paper. We tested at least 25 larvae from a composite of at least five females depending upon the availability of test plants and larvae. Leaves were replaced and feces removed as needed. The larvae were reared at room temperature (23.1 ± 1° C).

Test plants (Table 1) were selected using literature records and included reported hosts of *P. rutulus, P. eurymedon, P. glaucus,* and *P. multicaudatus.* In addition, test plants were selected from common western native and ornamental plants in the same genera or families (Essig 1926; Remington 1950; Jones 1951; Kendall 1957, 1964; Brower 1958; Emmel & Emmel 1963; Garth & Tilden 1986; Tietz 1971; Scriber & Feeny 1979; Scriber et al. 1982; Scott 1986). These plants were available locally and leaves were cut as needed.

Results

Survivorship of *P. rutulus* larvae on the test plants ranged from 0 to 78.4% with all larvae dying on 14 plant species (Tables 2 and 3). Larvae completed development on plants in nine families, including the Lauraceae (*Cinnamomum*

Table 3. Number of *P. rutulus* larvae tested, highest stage reached and abundance of non host plants.

Plant	Number larvae	Ate leaves	Highest instar[a]	Abundance[b]
Acer saccharinum[c]	27	none	1st	common
Alnus rhombifolia	55	much	2nd	very common
Cornus serica	35	much	3rd	common
Fragaria chiloensis	25	little	1st	common
Fraxinus dipetala	12	little	1st	uncommon
Magnolia accuminata[cd]	39	little	1st	rare
Persea americana[c]	27	much	2nd	uncommon
Ptelea crenulata	29	none	1st	uncommon
Quercus chrysolepis	25	none	1st	common
Rhamnus californica	56	much	1st	common
Ribes aureum	45	none	1st	rare
Rubus leucodermis	20	much	2nd	uncommon
Ulmus americana[c]	20	much	2nd	uncommon
Ulmus parvifolia[c]	14	little	1st	uncommon
Total	429			

[a] Larvae have five instars.
[b] See Table 2 for references.
[c] Exotic plant in California.
[d] Supported survival of first instar larvae (unpublished data).

camphora (L.)) and Magnoliaceae (*Liriodendron tulipifera* (L.)), believed to be the original plant families of the *glaucus* group (Monroe 1960). Our larvae completed development on 77.7% (14/18) of the *P. rutulus* hosts reported in the literature (Tables 1 and 2). Four reported host plants upon which they failed to complete development were *Alnus rhombifolia* Nuttall, *Persea americana* L., *Ptelea crenulata* Greene and *Quercus chrysolepis* Liebmann. Of those test plants selected from groups listed only by genus, only *Fraxinus latifolia* (Bentham) (1/7) supported complete development of the larvae. Larvae were unable to complete their development on species of *Acer, Magnolia, Rubus* and *Ulmus* casting doubt on their suitability as *P. rutulus* hosts. We were able to confirm the ability of *P. rutulus* larvae to complete development on most, but not all, plants previously shown to support survival of first instar larvae (unpublished data). Development was completed on *L. tulipifera, Alnus oregona* Nuttall, *Platanus californica* Bentham, *Populus fremontii* S. Watson., *P. tremuloides* Michanux, *Citrus limon* (L.), *Betula papyrifera* Marshall and *Tilia americana* L., but not on *Magnolia accuminata* (L.). As determined in this study the potential larval host range for *P. rutulus* includes plants from at least 15 genera in nine families (Table 2).

Survival of *P. rutulus* larvae on native western host plants tended to follow taxonomic lines. The five native western plants with the greatest larval survival rates (48.0–59.3%) are all in the Salicaceae. Next, are native western plants in the Rosaceae (23.1–31.7% survival), Oleaceae (14.7%), Betulaceae (8.0–14.0%) and Platanaceae (5.7%). Native *Salix hindsiana* Bentham and *Betula occidentalis* Hook do not follow this trend with larval survival rates of 3.8% and 3.3% respectively (Table 2).

Exotic plants exhibited variable suitabilities for *P. rutulus* larvae. Introduced poplars had the best (78.4% for *Populus nigra* L.) and among the worst (4.0% for

Populus alba L.) survival rates for *P. rutulus* larvae (Table 2). *Betula pendula* Roth was 9.3 times more suitable as a host than the native *B. occidentalis* while *Prunus armeniaca* L. allowed only one-half the larval survival of the native *Prunus* spp. Introduced *Syringa vulgaris* L. and *Ligustrum japonicum* Nuttall (Oleaceae) supported *P. rutulus* larvae at one-third to one-quarter the rate of *F. latifolia.*

Ability of the host plants to support complete development of *P. rutulus* larvae was not closely related to their relative abundance in central California (Tables 2 and 3). Several common (*Rhamnus californica* Eschscholtz and *P. californica*) to very common plants (*L. japonicum, S. hindsiana* and *A. rhombifolia*) either failed to support complete development of the larvae or had low larval survival rates, while several uncommon to rare plants (*Prunus lyoni* (East), *Populus angustifolia* James and *P. tremuloides*) supported high survival of the larvae (Tables 2 and 3).

Papilio rutulus larvae were able to complete development on a number of plants previously reported as hosts of the other *glaucus* group members. These include: *P. lyoni, Prunus virginiana* L., *Prunus ilicifolia* (Nuttall) and *A. oregona* for *P. eurymedon* (Jones 1951, Emmel & Emmel 1963, Scott 1986); *Malus sylvestris* Miller, *C. camphora, P. virginiana, C. limon, S. vulgaris, L. tulipifera, Amelanchier alnifolia* Nuttall and *P. tremuloides* for *P. glaucus* (Jones 1951, Scriber & Feeny 1979, Scriber et al. 1982); and *P. virginiana, P. ilicifolia, F. latifolia, L. japonicum,* and *A. alnifolia* for *P. multicaudatus* (Essig 1926; Jones 1951; Brower 1958; Kendall 1957, 1964; Tietz 1971; Scriber & Feeny 1979; Scott 1986).

Because of the significance of *P. rutulus* survival on *L. tulipifera* to evolutionary schemes within the *glaucus* group (Scriber 1986, 1988; Scriber et al. in press), we did a further experiment to insure that our results were not due to peculiarities of the plant or test procedures. Eighteen *P. g. canadensis* larvae from four females were tested on local *L. tulipifera* leaves and 15 larvae from these same females were fed *P. tremuloides* leaves as above. All larvae died in the first and second instar as expected on *L. tulipifera* (Scriber 1988, Scriber et al. in press), while 60% of their siblings completed development on *P. tremuloides.* The ability of some *P. rutulus* larvae (4/95) to utilize *L. tulipifera* as a host reflects a detoxication system which appears to be genetically based at a low frequency in the population and is not due to any peculiarities of the individual test plant or experimental procedures.

DISCUSSION

The extreme disparity in the survival of *P. rutulus* larvae on the exotic poplars suggests that the foliar chemistry of these plants differs significantly from that of their congeners. Phenolic glycosides are important constituents of poplar and willow leaves which greatly influence their utilization by herbivores (Palo 1984; Rowell-Rahier 1984; Tahvanainen et al. 1985; Lindroth et al. 1986, 1988). *Populus nigra* leaves have far lower levels of total phenolic glycosides (0.02%) than those of *P. alba* (2.5%), *P. tremuloides* (7.0%), or *Populus trichocarpa* Grey (16.0%) (Palo 1984). Although survival of *P. rutulus* larvae is highest on *P. nigra,* it is lowest on *P. alba,* despite this latter plant having only one-third to one-sixth the levels of total glycosides of *P. tremuloides* or *P. trichocarpa. Populus alba* leaves have at least one unique phenolic glycoside, grandidentanin (Palo 1984), which may account for this difference. The successful utilization of *L. tulipifera* by *P.*

rutulus larvae represents an interesting situation. Clarke & Sheppard (1955), Scriber (1986) and Scriber et al. (in press) failed in their attempts to rear *P. rutulus* larvae on *L. tulipifera,* but they were able to rear *P. rutulus* × *P. glaucus* hybrids on the plant. A similar situation exists among the subspecies of *P. glaucus. Papilio g. glaucus* is able to utilize *L. tulipifera* although *P. g. canadensis* cannot, but hybrids of these butterflies are able to do so (Scriber et al. 1982, Scriber 1986). The basis for this may rest in the ability to detoxify the sesquiterpene lactones present in *L. tulipifera* leaves (Lindroth et al. 1986, 1988). Brower (1958) and Scriber (1986) have suggested that the genetics involved in larval survival on *L. tulipifera* may be controlled by one or more dominant genes in *P. glaucus.* The situation in *P. rutulus* is less clear. Our data show 4.2% of exposed larvae surviving on *L. tulipifera.* This suggests that several genes are involved and that only larvae homozygous at all loci are able to survive on *L. tulipifera.* Hybridization experiments should be able to determine the mode of inheritance of the ability of *P. rutulus* larvae to utilize *L. tulipifera.*

Brower (1958) and Scriber (1986) have suggested that western swallowtails in the *glaucus* group have developed restricted and mutually exclusive larval diets with *P. rutulus* utilizing the Betulaceae, Platanaceae, and Salicaceae, *P. multicaudatus* the Oleaceae, Rosaceae, and Rutaceae and *P. eurymedon* the Rhamnaceae. These restricted and mutually exclusive larval diets in nature clearly cannot depend solely upon differential larval survival. *Papilio rutulus* larvae are capable of completing their development on many of the host plants of *P. eurymedon* and *P. multicaudatus* (Table 2). However, host plant utilization is a two step process that first involves oviposition on the plant and subsequent survival of the resulting larvae. We have little data on the ovipositional preferences of these butterflies in the field. We have found *P. rutulus* larvae on all the *Populus* spp. except *P. alba.* We have also found them on *Salix lasiolepis* and less frequently on *Platanus californica* in the Sacramento area. Larvae of *P. eurymedon* have been found only on *Ceanothus* spp. and *Rhamnus* spp. Complete resolution of how these western butterflies divide the available host plants must await further studies on the survival of *P. eurymedon* and *P. multicaudatus* larvae on various plants and data on the natural ovipositional preferences of the three butterflies.

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